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The Victoria University.

1901.

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DISSERTATION ON  
CERTAIN PHENOMENA  
REGARDING  
RED AND PALE MUSCLES.

AN EXPERIMENTAL AND HISTOLOGICAL RESEARCH.

*SUBMITTED FOR THE DEGREE OF M.D.*

BY

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LIVERPOOL:

W. H. LLOYD, PRINTER, 61, DALE STREET.



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## PREFACE.

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THE following work was carried out during the first six months of 1898, in the Physiological Laboratories of University College, Liverpool.

During the next two years an appointment as Medical Officer to a large Union Infirmary prevented its completion, and it was only during the autumn of 1900 that I had sufficient leisure to resume the work.

The idea of investigating the properties of red and pale muscles was suggested to me by Professor Sherrington, and I would like to take this opportunity of expressing my great indebtedness to him for kindly assistance and suggestion extending over all the period of my association with the Laboratory.

J. H.

7, RODNEY STREET,

LIVERPOOL, *January, 1901.*

## ARRANGEMENT.

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## INTRODUCTION.

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THE question as to the relative functions of the red and pale muscle fibres is by no means a settled one, and the object of this investigation has been to obtain more facts concerning the reaction of these two types to various stimuli, and also as to the character of their nerve supply.

It will be advisable first to epitomise as briefly as possible the facts hitherto observed concerning the red and pale muscles, taking in order first the histological differences, then the comparison of their contraction, both single and tetanic, and, finally, their distribution and its relation to the functions of each type.

The two essential elements in a muscle fibre are the contractile and non-contractile. The contractile consisting of fibrils disposed singly or in bundles, and embedded in the non-contractile, the ground substance, which supports and surrounds them, and is termed the sarcoplasm.

These two elements vary greatly in their relative amounts and distribution. In some fibres the contractile fibrils are disposed around the periphery of the fibre, whilst in others they are placed centrally, or as in the multinuclear mammalian cross-striated muscle they are distributed all over the fibre grouped in "muscle bundles."

The essential and important histological difference between the red and pale muscle lies in the relative proportion of the contractile element to the non-contractile.

The pale muscles have little, the red muscles have much sarcoplasm. They are, therefore, designated by some, plasmic and aplasmic muscles. The actual size of the fibres is said to differ in the two types. The pale, aplasmic being larger on section than the dark, plasmic. The cross striation is also said to be more marked in the pale, whereas the longitudinal striae are more distinct in the red, dark fibres.

Again, according to some, the distribution of the nuclei is different, the nuclei in the dark fibres being more numerous and frequently placed centrally, those of the pale being usually situated at the periphery under the sarcolemma.

It has also been stated that there is a difference in the arrangement of the capillaries.

In the dark, plasmic fibres the capillary network is more intricate, the number of cross branches is greater and these are much dilated, so that these fibres have a richer blood supply.

The dark, plasmic fibres are therefore smaller, more liberally nucleated, with a relatively greater capacity for blood than the pale, aplasmic, and possess a relatively much larger amount of sarcoplasm.

The importance of the last statement depends entirely on what we consider the function of the sarcoplasm.

It is generally admitted that the sarcoplasm is responsible for the nutrition of the fibrils embedded in it. Therefore, the greater the amount of sarcoplasm, the greater the possible nutrition of the contractile element in the fibre.

Microscopically the differences are obvious, being primarily those of colour. Where the two types are well marked, the red muscles stand out strongly from amongst the pale. We also notice in these cases that the red are, as a rule, the smaller in bulk.

The red coloration is not due only to the excessive amount of sarcoplasm and the larger blood supply, but the muscle is said to be coloured by haemo-globin and other colouring matters. So that, in some cases, the reddest muscles are not the most typically plasmic.

So much for the histological and naked eye appearance. When we consider the character of the single contraction in each case the difference becomes still more marked.



This difference was first noted by Ranvier<sup>1</sup> in 1874, who showed that the length of the twitch in the pale muscles of the rabbit was considerably shorter than that of the red, and that there was a corresponding difference in the latent periods, that of the vastus internus being one quarter that of the semi-tendinosus.

The character of the contractions as shown in myograms was also noted. The height of the twitch from the pale muscle being much greater than that from the red, and the acme of the contraction being rapidly reached in the case of the pale, while that from the red very slowly attained its maximum.

<sup>2</sup> Cash compared the various muscles in the frog and tortoise, demonstrating corresponding differences in their myograms and length of contraction.

Marked as the differences were when single stimuli only were used, still greater were found on applying repeated stimuli so as to obtain tetanic contraction.

<sup>3</sup> Grützner showed that the work done by the red muscles during tetanus was much greater than that of the pale.

He also demonstrated that the ratio between the height of a twitch to that of tetanus was much less in the pale than in the red.

He also found that it was much more difficult to fatigue the red muscles than the pale, and that, following tetanic contraction, the excitability of the pale muscles was considerably more lowered than that of the red muscles. He therefore designated these plasmic, dark muscles "Tetanus Muscles."

<sup>4</sup> Rollett investigated the muscles of the *Dytiscus* and *Hydrophilus*, comparing the sluggish muscles of *Hydrophilus* with the excitable quick

<sup>1</sup> Ranvier. *Archiv. de physiol. norm. et pathol.*, 1874. *Leçons de l'anatom. générale, Paris*, 1880.

<sup>2</sup> Cash. *Du Bois Reymond's Archiv.*, 1889. *Supplementband*.

<sup>3</sup> Grützner. *Pflüger's Archiv.*, 47 Band und 48. *Pflüger's Archiv.*, 41 Band, *Breslauer ärzliche, Zeitschr.*, 1883.

Rollett. *Sitzungsber d. Wiener Academie*, lxxxix. iii *Abth.*, 1884.

*Ibid*, xcvi, iii *Abth* 1889.

*Denkschriften der mathem.—naturwiss. Klasse der kaiserl Academie der Wiss. in Wien*, liii.

muscles of the *Dytiscus*, showing the poor staying power of the *Dytiscus* in contrast with the powerful, prolonged contraction of the *Hydrophilus*.

<sup>1</sup> Richet investigated more particularly the crab, obtaining similar results.

In the rabbit, Ranvier, <sup>2</sup> Kronecker, and <sup>2</sup> Stirling demonstrated the marked difference in the number of stimuli per second required to induce tetanus. The pale requiring 20 to 30 stimuli per second, and the red only 10.

The distribution of these two forms of muscle fibre presents many points of interest. In man and in most mammals both are found in the same muscle, the red fibre preponderating; the muscles in man tending to react as red muscles though containing both forms of fibre.

In many animals, however, the differentiation and arrangement is much more defined, certain of the muscles being practically entirely composed of pale, others of red fibres only.

It is in cases such as these that we can compare the typical reaction of the two types to perfection.

The rabbit is a well-recognized example, most of its thigh being formed of extremely pale muscles, with the deep-red, semi-tendinosus embedded in them.

Speaking generally, we find the pale fibres predominating in the amphibia, and the red in birds and onward.

But in each of these two classes there are instructive and interesting exceptions. For example, the breast and back of a hen are composed mainly of pale fibre, the leg muscles of red fibred muscle. Compare this with the breast muscles of a pheasant or pigeon, and you find the breasts of the latter are almost entirely composed of red fibres.

In the batrachia again the throat muscles are usually red.

This irregular distribution is interesting chiefly in its relation to the supposed function of the plasmic fibres.

Grützner, as we have before noted, considers them on account of their physiological characteristics as tetanus muscles, and shows that the red

<sup>1</sup> Ch Richet *Physiologie des muscles et des nerfs*. Paris 1882.

<sup>2</sup> Kronecker and Stirling. *Ludwig's Arbeit*, Leipzig, 1877. Du Bois Reymond *Archiv.*, 1878



muscles in an animal are those which usually have the hardest and most prolonged work.

They are the muscles which have to hold on—which can best resist fatigue. As Ranvier showed in the case of the triceps humeri in the rabbit which consists of both pale and red fibres, that, in stimulating it, it first served up contractions like a pale muscle, but later, when the pale element was fatigued, the response to stimulation was that of a red muscle.

The pectorals of a hen are pale, and their work is spasmodic and fitful, while those of a pigeon are almost entirely composed of red fibres, and the work they have to perform is arduous and prolonged.

Examples illustrating this point could easily be multiplied, but the above are sufficient. As Biedermann says, “The elements of those muscles which serve the most persistent or most strenuous action are richest in sarcoplasm”. . . . “there seems, therefore, to be a direct relation between the extension and force of the contractile fibrils and the bulk of the surrounding protoplasm.”

This brings us back to the idea that it is the relative amount of the sarcoplasm which is the essential and vital difference between the two forms of muscle fibre.

The experimental work to follow bears out this view, namely, that there is some essential difference in the muscles themselves which enables the red muscles to survive and work without a blood supply for a much longer period than the pale, and that that difference is most probably to be found in the relative amounts of the sarcoplasm.



## PLAN OF WORK.

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- 1.—To obtain normal tracings from red and pale muscles.
- 2.—To obtain tracings from the same muscles with animal under the influence of curari.
- 3.—To observe the effect of cutting off the blood supply from the red and pale muscles.
- 4.—To observe and record the differences in the reflex excitability of the red and pale muscles.
- 5.—To compare the nerve supply of the red and pale muscles.
  - (a)—In relation to absolute number of fibres.
  - (b)—In relation to the size of the nerve fibres to each form of muscle.
  - (c)—The number and size of the afferent fibres to red and pale muscles.
- 6.—To examine the motor end plates of red and pale muscles (Sihler's process).
- 7.—To examine and compare the muscle spindle in the red and pale muscles.

### Choice of Animal.

It was necessary to find an animal in which the two forms of muscle to be examined were present in a typical condition.

Both the frog and the cat possess red and pale muscles, but their red muscles contain quite an appreciable amount of pale fibre.

The rabbit seemed to be a suitable animal, and showed a very marked contrast in the composition of several of its muscles. There was one objection, however, against employing rabbits, and that is that they are so easily killed by chloroform or shock, and in operative work are so liable to sepsis. On this account I met with failure after failure in the operative portion of my investigation.

Still the rabbit appeared to be the best animal for the purpose, and was used throughout. Three of its muscles were employed as types of the red and pale muscles. These were the semi-membranosus, semi-tendinosus, and the soleus.

The first being a very pale, fibred muscle, and the other two as markedly red.

The semi-membranosus and semi-tendinosus have a very similar origin and insertion, action, and nerve supply, so were well fitted for comparison.

The soleus was on the other hand a flexor of the foot.

Another point in favour of using these three muscles was that they could all be stimulated simultaneously through the sciatic nerve.

\* *M. semi-membranosus.* Ursprung : Vom Tuber ischii, bedeckt vom M. biceps, nach vorn vom M. gluteus Maximus, ferner von einem fibrösen Blatte, welches dem Ursprungstheile des M. biceps femoris and zum Theil des M. adductor magnus aufliegt, Kräftiger, fleischiger, spindelförmiger Muskel, verläuft schräg abwärts und medianwärts und geht in eine breite, dünne Sehne über. Die Breite des Muskels beträgt etwa das Doppelte seiner Dicke. Insertion : Die Sehne befestigt sich gemeinschaftlich mit der des M. gracilis am Ende des oberen und Anfang des mittleren Drittels der Tibia. Die hinteren Faserzüge gehen in eine lange, nach unten sich verjüngende Sehne über, die in nach vorn convexem Bogen zur Achillessehne herabsteigt, mit welcher sie sich verbindet.

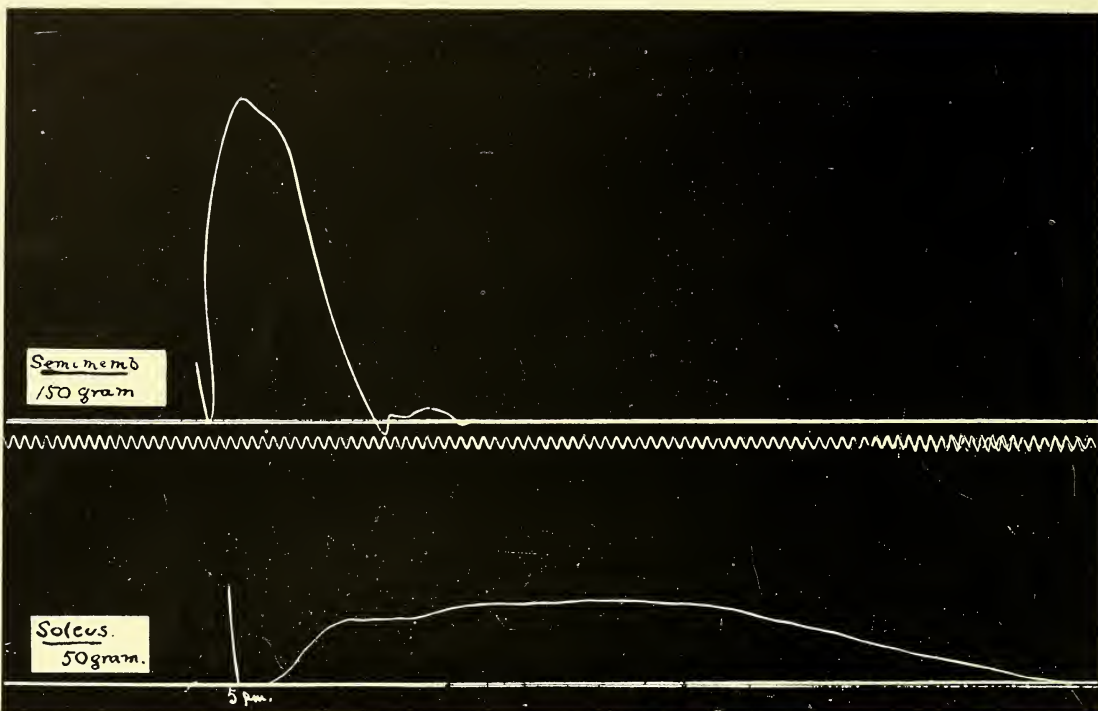
*M. semi-tendinosus.* Ursprung : Tuber ischii, durchbohrt den M. adductor magnus, der ihn von allen Seiten umgibt. Auf Querschnitten ist sein röthlicher Muskelbauch in dem weisslichen Fleisch

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\* Extract from Krause, *Anatomie des Kaninchens*, p. 119-121.

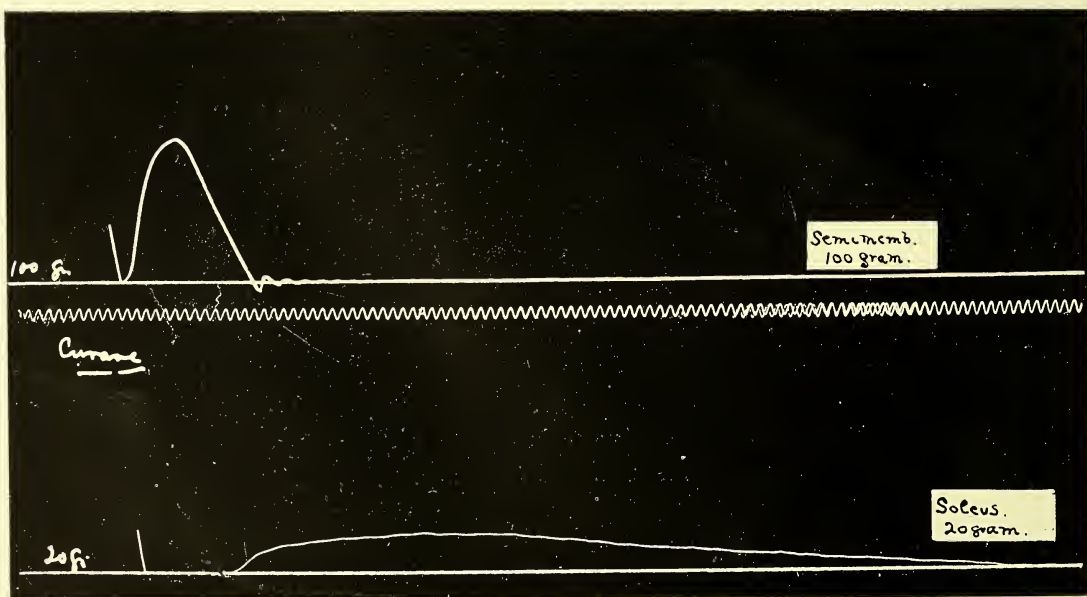


# PLATE I.



Tracings from normal muscles, semi-membranosus (pale), and soleus (red). Rabbit. Time marking,  $\frac{1}{100}$ ". Stimulus—single break shock.

# PLATE II.



Tracings taken from curarised Rabbit. Semi-membranosus (pale). Soleus (red). Stimulus—single break shock.



des M. adductor magnus auffallend. Insertion : Mittelst einer langen Sehne an den medialen Condylus tibiae, oberhalb des Ursprungs des M. extensor digit 1. proprius.

*Muskeln an der hinteren Seite des Unterschenkels.*

*M. triceps surae.* Ursprung : Mit drei Portionen, von denen die eine : der M. gastrocnemius medialis, vom Condylus medialis, die andere : der M. gastrocnemius lateralis, vom Condylus lateralis femoris, sowie vom oberen Ende der Tibia, die dritte : der M. soleus, vom Capitulum fibulae unterhalb des Condylus lateralis tibiae entspringt. Die beiden oberflächlichen Köpfe, von denen der laterale der stärkere ist, convergiren und vereinigen sich noch am oberen Drittel der Tibia fleischig, bald aber sind sie nur durch einen Sehnenfortsatz verbunden, welcher von dem Tendo Achillis sich zwischen sie hineinschiebt. Der dritte, unter dem M. gastrocnemius lateralis liegende Kopf, verschmilzt in der Mitte der Tibia mit demselben ; doch reicht seine Muskelsubstanz weiter abwärts als die der Mm. gastrocnemii. Der M. triceps surae in seiner Gesamtheit stellt einen bedeutenden kräftigen Muskelkörper dar, welcher die ganze hintere Fläche der Tibia bedeckt und medianwärts in der Mitte den M. plantaris etwas zum Vorschein kommen lässt. Insertion : Die gemeinsame Insertionssehne ist der mächtige, rundliche Tendo Achillis. Sehnenfasern vom Tendo Achillis erstrecken sich mehr oder weniger weit auf die in diese Sehne übergehenden Muskeln, ganz besonders sieht man auf der vorderen Fläche des M. gastrocnemius medialis eine schräge Fortsetzung derselben, welche bis zur Mitte des Muskels hinaufreicht. Die Achillessehne legt sich auf das überknorpelte hintere Ende des Calcaneus und befestigt sich an den hinteren Theil der plantaren Fläche desselben.

**Comparison of myograms obtained from normal red and pale muscles of rabbit with those from curarised rabbit.**

THE first step was necessarily to obtain normal tracings from the red and pale muscles. The semi-membranosus and soleus of the rabbit were used. The stimulus being a single break shock. Plate I is a reproduction of one of the tracings.

It show very well the typical differences between the contractions of the two forms of muscle. In this particular experiment the contraction of the pale muscle lasted .15 of a second, the contraction of the red .70 of a second.

The sudden, short contraction of the pale is in marked contrast to the slow and prolonged contraction of the red muscle.

The ratio here was as 1 is to 4.66, but in some experiments it reached as much as 1 to 12, and as low as 1 to 3. The ratio 1 to 3 was the lowest obtained with the muscles in a normal state. Kronecker and Stirling give the normal ratio of the rabbit's red and pale muscles as below 1 to 3, but the numerous tracings I obtained certainly gave a much higher average difference in the duration of contraction.

The next point to be demonstrated was to what extent the muscle, and also to what extent the nervous apparatus was responsible for this marked difference in duration and character of contraction.

A rabbit was prepared as for previous experiment and then curarised, and from this animal's muscles contractions were evoked by single break shocks, applied directly to the muscle. Plate II records the results.

If one compares plate II—the tracings taken from the curarised animals, with plate I—the normal, it is obvious that there is no essential difference.

There is the same characteristic, sudden, short, contraction of the pale, and the slow, prolonged contraction of the red muscle, although all stimulation of their nerves and nerve endings had been rendered impossible by the curari.

The conclusion is, therefore, that the differences in contraction are due undoubtedly to the structural differences in the actual muscle fibres, independently of any possible variation in the nerves or nerve endings.

### **Experiments relating to the effect of cutting off the Blood Supply to the Red and Pale Muscles.**

With regard to the question of the effect of cutting off the blood supply from the different muscles, I have in all performed seven experiments.

The method of experiment was as follows, the following description holding good in each case, except where there is a definite mention of difference :—

A 50 per cent. solution of chloral hydrate was first injected under the skin of the rabbit, the amount varying with the weight of the animal, 3 to 3½ grains of chloral being used for every pound of rabbit.

The rabbit was then anæsthetized and the spinal cord carefully exposed and divided in the lower thoracic region. The bleeding generally ceased on applying gentle pressure.

The muscles and skin were then drawn together by sutures.

The abdominal cavity was next opened by a median incision, extending two or three inches from the pubes upwards. The intestines were held out of the way with swabs moistened with warm saline.

The peritoneum covering the aorta and inferior vena cava was broken through, and a blunt, curved needle passed round the aorta and inferior vena cava; by this a ligature was drawn round the vessels and the first half of a reef knot was loosely tied. The ends of the ligature were left hanging out of the abdomen, and the abdominal walls were drawn together by sutures.

The soleus and semi-membranosus muscles and sciatic nerve were then carefully exposed and all bleeding points secured.

The sciatic nerve was divided high up on a level with the upper portion of the ischial tuberosity.

There is a small artery and vein to the soleus accompanying its nerve, and towards the ischial origin of the semi-membranosus muscle on the under surface, the surface looking towards the bone, is a fairly large artery entering the semi-membranosus.

These vessels were preserved when freeing the muscles.

The rabbit was then fixed to a stage and the distal ends of the muscles attached to levers. After recording a normal tracing on a slowly revolving drum, the aorta and inferior vena cava were pulled on tightly by means of the ligature, which was also twisted, and to which a weight of 150 to 200 grammes was fixed to sustain the tension.

Following this, tracings were taken at regular intervals, the muscles in the meantime being bathed in warm, normal saline.

The stimulus in the first three experiments was indirect, the distal end of the divided sciatic being stimulated by break shocks, but in the other four, the muscles were directly stimulated by break shocks, the same current passing through both muscles.

In the following experiments sol.=soleus; s.m.=semi-membranosus.

EXPERIMENT 1. Jan. 13th. Buck rabbit,  $4\frac{3}{4}$  lbs. Chloral, 16 grs. The ligature passed behind aorta only. Stimulus 7.5 cm. Break shock, electrodes applied to sciatic nerve.

Weight on s.m. lever—150 grammes over pulleys-

„ sol. „ — 50 grammes direct.

Tracings every  $1\frac{1}{2}$  minutes on slow drum.

The aorta was supposed to have been occluded at 3 hrs.,  $8\frac{1}{2}$  mins., p.m. ; both muscles, however, went on contracting quite vigorously for one hour and fifty minutes.

The ratio of length of contraction changed somewhat during that period. Commencing with a ratio of 1 to 4·6 at  $3-8\frac{1}{2}$  p.m., that is, the red muscle twitch contraction was 4·6 times the length of the pale twitch, it became

1 to 4 at 3-27 p.m.

1 to 4 at 4-27 p.m.

1 to 3·8 at 3-47 p.m.

1 to 4·08 at 4-55 p.m.

1 to 3·4 at 4-7 p.m.

1 to 4·8 at 5 p.m.

and then the red soleus suddenly ceased to contract, the pale reacting vigorously to the breakshock and continuing to do so for some time.

EXPERIMENT 2. Jan. 14th. Buck,  $5\frac{1}{2}$  lbs. Chloral, 18 grs. Ligature passed behind aorta and inferior vena cava. Stimulus, 7·5 cm. Breakshocks to sciatic nerve. Weights as before. Normal tracing on rapid drum. Ratio, 13 to 67.

3-30 p.m.—Vessels occluded. 100 gramme weight fixed to ligature and twisted.

3-52 p.m.—Pale muscle gave no record though it was observed to twitch slightly.

3-57 p.m.—Weight removed from ligature and ligature untwisted. Blood flow had evidently returned to the muscle, because it began to bleed at several points. The pale s.m. began to give several contractions which were recorded on the tracing.

4-41 p.m.—The ligature was again twisted and weighted.

5-3 p.m.—There was no contraction of the pale s.m. visible, the last recorded contraction being at 4-50 p.m.

The red muscle continued contracting steadily till 6-1 p.m., when it suddenly failed. Vide tracing.

EXPERIMENT 3. Jan. 19th. Doe,  $4\frac{1}{2}$  lbs. Chloral, 18 grs., and 5 grs. later on in experiment. Ligature round aorta and inferior vena cava. Sciatic stimulated. Weights as before. Marked reflex excitability of muscles noted. 1st tracing taken 1-35 p.m. ; ratio, 1 to 5. Aorta and inferior vena cava tightened 2-6 p.m.

In this experiment the s.m. did not absolutely cease to respond on occlusion of the vessels, but continued to give small, flickering responses almost as long as the red.

The *lift* of the contraction was practically nil, however, at the end of about thirty minutes.



The soleus continued to give good contractions till 3-4 p.m., when it suddenly ceased to respond.

Loosening the ligature on the vessels had no effect in this experiment.

EXPERIMENT 4. Jan. 20th. Doe,  $4\frac{3}{4}$  lbs. Chloral, 16 grs. Weights as before. Ligature round aorta and inferior vena cava. In this experiment the vessels were supposed to have been completely occluded at 1-50 p.m., but I am of opinion that the occlusion was neither complete nor continuous, for, although the s.m. gradually diminished in power of lift for thirty minutes, it then again regained its strength.

The length of the contraction of the soleus and its lifting power diminished somewhat after the first half-hour, and, at the end of an hour, was only half of what it was at the commencement. It then suddenly ceased contracting to the usual stimulus of 7.5 cm.

The electrodes were next applied directly to the soleus and it responded vigorously. Accordingly the muscles were stimulated directly, the same current passing through both. The weight of 50 grammes attached to the lever of the soleus muscle was replaced by one weighing 30 grammes.

Three normal contractions were then taken, and the aorta and inferior vena cava absolutely occluded by considerable tension applied to the ligature. This was done at 3-19 p.m.; following it there was an immediate change in the response of the s.m. There was an even and gradual diminution of the height and length of the tracings, till at 3-42 p.m. there was no response, whereas the red was acting vigorously, the actual lift being greater than at 3-19 p.m., although the length of the contraction was not so great.

The tension was removed from the vessels, but no change occurred.

The soleus continued to respond till 5-44 p.m., that is, 145 minutes from the definite occlusion of the aorta, and 234 minutes from the beginning of the experimental stimulation.

EXPERIMENT 5. January 23rd. Buck, 6 lbs. Chloral, 18 grs. Prepared as January 20th. Stimulus, 8 cm. *indirect*. Weights, 200 grammes to s.m., 50 grammes sol. At 3-27 p.m., two normal tracings recorded on a fast drum:—s.m., .12" to .13"; sol., .515" to .61".

At 3-29 p.m., the tension was applied to the aorta and inferior vena cava, and tracings taken periodically on a fast drum. As no definite change had been noticed in the contractions by 4-4 p.m., extra pressure was put on to the vessels. Following this the character of the pale muscle contractions began to change, the lift distinctly

and definitely diminished and the length of the contraction became less. The red soleus was recording well, but at 4 32 it suddenly ceased to give a contraction, although five minutes previously it recorded a contraction of '63" in duration.

The electrodes were then applied to the muscle directly, with the result that the soleus served up good contractions. At 4-49 p.m., the animal was noticed to be dying, and, as on *post mortem* examination, the abdomen contained large clots of blood, the vessels had probably been lacerated at 4-4 p.m. and the animal had bled into its abdominal cavity.

4-50 p.m. —Rabbit dead.

By 4-55 p.m. the pale s.m. refused to respond, having rapidly failed after the death of the rabbit. The red soleus was then contracting '65" to '70", and continued to contract vigorously. At 5-28 p.m. the contractions became somewhat more prolonged, and the lift decreased. This prolongation of the contraction increased so much that, by 5-51 p.m., the records were four or five times as long as at the commencement.

EXPERIMENT 6. June 7th. Strong buck, 6 lbs. Chloral, 14 grs. Aorta and inferior vena cava ligatured loosely in two places. Stimulus directly to muscles. At 3-30 p.m. aorta and inferior vena cava occluded. At 4-30 p.m., the s.m. gave its last contraction just strong enough to be recorded. The soleus at this point acting as vigorously almost as at first, the lift being a little less, and the duration of the contraction somewhat increased.

At 4-55 p.m. the red soleus failed, that is, 35 minutes after the failure of the s.m., the soleus failed slowly.

EXPERIMENT 7. June 10th. Doe. Chloral, 12 grs.

The occlusion of the aorta in this case did not appear to have any very marked effect on the s.m.

The soleus, however, slowly diminished in lifting power and the duration of its contraction. The lift of the s.m. also diminished somewhat, but again recovered.

At this point the rabbit made some violent movements on the stage and ruptured the aorta and inferior vena cava, consequently bleeding to death.

For an hour or so after death both the soleus and semi-membranosus contracted in response to direct stimulation.



### Discussion of above Results.

In considering these seven experiments there are several points of interest. One of these, and the first we will notice, is the conduct of the red muscle to repeated indirect stimuli.

In five out of the seven experiments, in fact, in every case in which indirect stimuli was employed, it was found that the red muscle suddenly ceased to respond to the usual stimulus. The point of interest is the suddenness of the refusal to respond.

In exp. 1, sudden failure of red—1 hr., 50 min., after lig. of vessel.

„	2,	„	„	2	„	30	„	„	„
„	3,	„	„	1	„	5	„	„	„
„	4,	„	„	1	„	4	„	„	„
„	5,	„	„	1	„	3	„	„	„

In each of these cases, the contraction from the red soleus previous to its refusal to respond was a good one. This vigorous contraction being followed by an absolutely negative result, the muscle not even twitching.

In experiment 5, the last contraction of the soleus to indirect stimulation lasted '63". Five minutes after, it absolutely refused to respond.

There is a great difference in this method of cessation to that when the muscles are stimulated directly. In experiments 4 and 5, the electrodes were applied directly to the muscles on the red failing to respond to indirect stimulation. The same stimulus passed through both muscles.

Under these conditions the red again replied vigorously, and, with this method of stimulation, failed slowly, the duration of the contract increasing, the lift diminishing, and the latent period becoming lengthened.

This slow failure was observed in experiments 4, 5, and 6.

There was not an instance of sudden failure in the pale muscles, although acting under exactly similar conditions to the red.

In experiment 1, two hours after the supposed ligature of the vessels, the pale s.m. was acting well, in contra-distinction to the red, which had suddenly failed to respond.

In experiment 4 again, where the red failed in one hour and four minutes, the pale, after the same time, stimulated by the same shocks, and under similar conditions, was responding almost as vigorously as at first.

The cause for this difference in the two muscles lies most probably in the nervous apparatus, and we have found that there is a very definite difference between the size of the nerve fibres to the red and to the pale muscles. It is possible that the smaller sized fibres are less able to bear the slight changes of temperature and the exposure than the larger, though I cannot understand how the actual conductivity should be seriously altered.

It may possibly be due to some difference in the nerve endings, but here I was not able to find any cause, the motor end plates (as stained by Sihler's process), being practically similar in the two muscles.

Whatever the cause may be, the fact remains that the red muscle suddenly failed in every case of prolonged indirect stimulation, whilst the pale muscle failed gradually under exactly similar conditions.

### **Effect of Stoppage of Blood Supply.**

The results have been rather conflicting, but I think that one is justified in one or two conclusions. The effect of complete ligature of the aorta and inferior vena cava seems undoubtedly to have a much greater effect on the pale muscles than on the red. In fact, one might say that its influence on the red is of only the slightest character.

In appendix (A), I have given a detailed account of experiment 2, because it seems to me typical, showing rapid failure of the pale s.m. twenty-two minutes after cessation of blood supply—again four minutes after taking the pressure off the aorta a slight response was obtained from the pale s.m. The aorta remained unoccluded for forty minutes, the s.m. giving small contractions during that period, and for twenty-three minutes following a second occlusion of the aorta.

In this experiment, there is no doubt that the muscle again received its blood supply on the loosening of the ligature round the aorta, because the

## APPENDIX (A).

*Experiment 2 in detail. Showing effect of cutting off blood supply from Red and Pale Muscles.*

Distance of Secondary Coil.	Time of Day. HRS. MINS.	Weight on Pale Muscle, grammes.	REMARKS.
7.5 cm.	3-25	150	{ $\frac{5.0}{10.0}$ " being average length of time of contraction of Soleus — "Red" muscle
"	3-28	"	
—	<b>3-30</b>	—	<b>Aorta and Inferior Vena Cava occluded.</b>
"	3-32	"	{ .27" .30" .28" .29" .37" } .282" = Average length of Red muscle contraction.
"	3-44	"	
"	3-46	"	
"	3-48	"	
"	3-50	"	
"	<b>3-52</b>	"	<b>No record from Pale muscle.</b>
7 cm.	3-54	"	Seen to twitch slightly.
6 cm.	<b>3-56</b>	"	<b>No record from Pale muscle.</b>
—	3-57	—	Weight <i>removed</i> from Aorta and Inferior Vena Cava.
"	3-59	"	No record from Pale muscle.
"	4-1	"	{ Small contraction of Pale muscle recorded. Blood flow evidently returned because the muscles are beginning to bleed
"	4-23	"	
"	4-27	100	Slight contraction of the Pale muscle
"	4-29	"	{ Average length of Red muscle contraction .353" } { .42" .37" .32" .35" .33" .33" .37"
"	4-31	"	
"	4-34	"	
"	4-37	"	
"	4-40	"	
—	<b>4-41</b>	—	<b>Aorta and Inferior Vena Cava again occluded.</b>
7.5 cm.	4-49	"	
6 cm.	4-50	"	
"	4-53	"	
"	4-55	"	
"	5-0	"	
"	<b>5-3</b>	"	<b>Practically no contraction of Pale muscle visible.</b>
"	5-6	"	do.
"	5-9	"	do.
"	5-12	"	do.
"	5-15	"	do.
"	5-18	"	do.
"	5-21	"	do.
"	5-30	"	.38"
"	5-36	"	.41"
"	5-41	"	.44"
"	5-46	"	.52"
"	5-51	"	.47"
"	5-56	"	.52"
"	6-1	"	.46"
"	6-6	"	<b>Sudden failure of Red (Soleus) to record; only faint</b>
4 cm.	6-14	"	No record. [contraction visible.

muscle substance began to bleed at several points. In some of the other experiments, however, loosening the ligature had no recuperative effect, and, on examining these rabbits *post mortem*, the vessels were found occluded by clots.

Tabulating the results of four of the experiments, we get

Exp. 2 (a), failure of pale s.m.—22 mins. after occlusion of vessels.					
„	(b),	„	23	„	„
„	3	„	30	„	„
„	4	„	23	„	„
„	6	„	41	„	„

In each of these cases, as we have seen, the red continued to contract vigorously for some considerable time after the failure of the pale. The average length of time in these four experiments being under thirty minutes as the time during which the s.m. will contract after complete cessation of blood supply.

The effect upon the red soleus was rather different in the various experiment. In experiment 2, the contractions of the soleus were shortened and no diminution in its lift. In experiment 4, the contractions of the soleus were again shortened and the lift increased. In experiment 5, following the death of the rabbit, the contractions of the soleus were shortened for the first twenty minutes, the lift remaining about the same. This was followed by a decrease in the lift and considerable lengthening of the contraction—slow failure of the muscle.

We may take it, therefore, that the pale muscle is most dependent upon a good supply of arterial blood for efficient contraction, and, failing that, it soon loses its power to respond to stimulation.

The red, on the other hand, can contract for a considerable length of time, even though deprived of all fresh supply of blood, the only immediate effect of such deprivation being to shorten the length of the contraction, the actual lifting power of the muscle remaining unimpaired.



### Comparison of the Reflex Excitability of the Red and Pale Muscle.

On the reflex excitability of the red and pale muscles twelve experiments were carried out. The muscles made use of were again the semi-membranosus, the semi-tendinosus, and soleus.

The sensory nerve stimulated in order to evoke the reflex response was the Posterin Tibial.

It was exposed at the side of the Tendo Achilles, and the stimuli employed were mechanical injury—either pinching or ligaturing—and the application of the Faradic current.

The semi-tendinosus is more definitely a red fibred muscle than the soleus, and its action is much the same as that of the semi-membranosus, both muscles arising from the ischial tuberosity and being inserted into the tibia; the semi-tendinosus into the posterin and external portion of the head, and the semi-membranosus by a long fascial expansion into the head and tuberosity. It is important to note that there extends downwards from this broad expansion a definite tendinous strip ending in the tendo achilles—so that contraction of the semi-membranosus acts partially as an extensor of the foot, and thus to some extent is comparable with the soleus. — See extract from *Krause*.

The outcome of these experiments is to establish the fact that there exists a very great difference in reflex excitability between the two forms of muscle.

The pale semi-membranosus responded vigorously and rapidly to stimulation of the posterior tibial, whereas the red muscles soleus and semi-tendinosus gave either no reply or only a feeble, sluggish contraction.

This is interesting in relation to Grützner's views regarding the function of the two forms of muscle. As we have already noted, he terms the red sarcoplasmic muscles "tetanus muscles." It is obvious that this type of muscle is not adapted to take at any rate the initial part in a reflex response, which to be of practical service must in many cases be rapid.

It seems therefore quite in keeping that they should be wanting in a quality the possession of which would be of no practical value.

Eleven experiments were carried out comparing the reflex excitability of the semi-tendinosus and the semi-membranosus, in every one of which the semi-membranosus gave a full, rapid, and vigorous reply.

On only one occasion (experiment 8) did the semi-tendinosus respond—the response being of the most feeble character, and this being obtained, not under normal conditions, but only after the animal's reflex excitability had been markedly increased by strychnine.

Strychnine was employed in four other of these experiments (experiments 6, 7, 9, 10). The exaggerated response from the semi-membranosus showing the heightened reflex excitability, but in spite of this the semi-tendinosus remained quite irresponsive.

Seven experiments were carried out on the reflex excitability of the soleus (exps. 1, 2, 4, 5, 10, 11, 12), in four of which (exps. 1, 2, 4, 5), there was absolutely no response, and the contractions in the other three, *vide* 10, 11, 12, were very poor ones. In experiment 10 the rabbit was under the influence of strychnine, yet the reflex reply from the red was not vigorous.

In experiment 11, it was found necessary to apply a much stronger stimulus to the posterin tibial nerve, in order to evoke a reply from the soleus, than that necessary to evoke a response from the semi-membranosus; whilst in experiment 12, the same condition obtained. In this case it was also noted that severe pinching of the posterior tibial elicited no response from the soleus, though starting a strong contraction in the semi-membranosus.

I do not think that this difference in reflex excitability can be explained on the ground of marked difference in the action of the muscles we have been observing. The semi-tendinosus must, so far as I can gauge its action, be classed with the semi-membranosus as a flexor of the leg on the thigh, and also both muscles tend to rotate the tibia inwards.

Again they have a common action in extending the hip.

The semi-tendinosus is almost imbedded in the adductor magnus in its origin from the ischial tuberosity, and here again the pale adductor magnus replies vigorously to the stimulation of the posterin tibial, whilst the red muscle practically imbedded in it is motionless and flaccid.



The adductor magnus and the semi-tendinosus are both extensors of the hip and might be expected to act in unison.

The soleus and semi-membranosus on the other hand might be considered as unsuitable for comparison, and in fact it was because of this that I turned to the semi-tendinosus after the three first experiments with the soleus, in each of which I failed to get a response from the red. My failure I attributed to the fact that I was comparing a flexor of the knee with an extensor of the ankle, and therefore I sought for a muscle which had a similar action to the pale semi-membranosus. However, it was the soleus which gave the only positive reflex contractions from the red fibred muscles.

I think therefore that as we earlier decided that the difference in the character of contraction was due to the structure of the muscle, so again we are driven to the conclusion that the difference in the character of the response to reflex stimulation is also intrinsically muscular ; the pale fibred muscle responding immediately and vigorously, whilst the red under exactly the same conditions, and with exactly the same action (S.T. AND S.M.) either fails entirely to reply or responds feebly and ineffectually.

It would have been interesting to have exposed the cerebrum of the rabbit and stimulated its cortex in order to see what were the movements in which the semi-tendinosus participated, and in what respects its action differed from or agreed with that of the semi-membranosus.

The cortex of the rabbit is unfortunately ill fitted for such an experiment, and it was not attempted.

### Experiments on reflex excitability.

EXPERIMENT 1. FEB. 15. Cord divided under chloroform. Soleus and semi-membranosus exposed. Post. tibial nerve exposed at each ankle. The post. tibials were then stimulated by Faradisation, and a good reflex contraction obtained from the semi-membranosus, but no reply from soleus.

$\frac{1}{2}$  to  $\frac{3}{4}$  of a grain of strychnine in solution was then injected hypodermically.

On stimulating the post. tibial, it was then found that the reflex excitability of the semi-membranosus was much increased, whilst that of the soleus was apparently unaltered.

The animal finally died in a general convulsion, not started by any known stimulus. In this final convulsion both muscles contracted vigorously.

EXPERIMENT 2. FEB. 22. Cord divided in lower dorsal region under chloroform. Semi-membranosus and semi-tendinosus on right side carefully exposed. Right post. tibial nerves exposed as in exp. 1. Stimulation of post. tibial gave only faint reflex contractions in semi-membranosus. No reflex in semi-tendinosus.

Left post. tibial next stimulated. The left knee was vigorously and strongly flexed, and a faint reflex contraction noticed in semi-membranosus of right side, nothing in semi-tendinosus.

The semi-tendinosus and semi-membranosus were then rapidly exposed on the left side, disregarding any but excessive bleeding. The left semi-membranosus then gave strong reflex contraction to stimulation of either post tibial, especially the left. Not the faintest contraction was noticed in the left semi-tendinosus.

The left soleus and gastrocnemius were next rapidly exposed. No reflex contraction could be obtained from them.

EXPERIMENT 3. FEB. 24. Cord divided fairly high up under chloroform. Rabbit then fixed on stand and right semi-membranosus and semi-tendinosus rapidly exposed and attached to levers.

(1)—The right post. tibial stimulated mechanically by pulling on it by thread attached to it. Semi-membranosus responded by vigorous contraction. Semi-tendinosus gave no reply.

(2)—Faradisation next tried to the right post. tibial, the result being the same. Vigorous contraction from semi-membranosus; no contraction in semi-tendinosus.

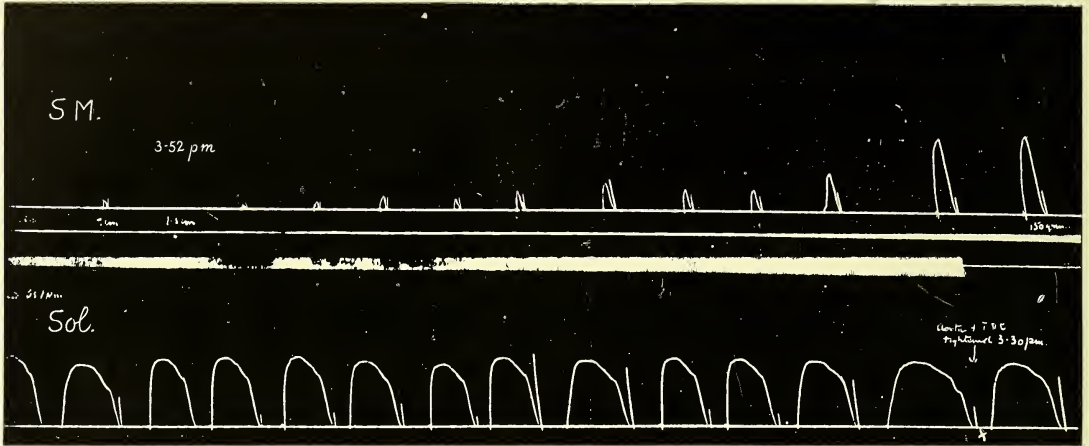
EXPERIMENT 4. MARCH 3rd. Rabbit prepared as before.

(1)—Right and left post. tibial nerves pinched. Semi-membranosus of right side contracted in each case. Semi-tendinosus and soleus did not contract in either case.

(2)—Right post. tibial stimulated by tying a thread tightly round it. Semi-membranosus, right side, gave a marked and strong contraction. Not a flicker in soleus or semi-tendinosus.

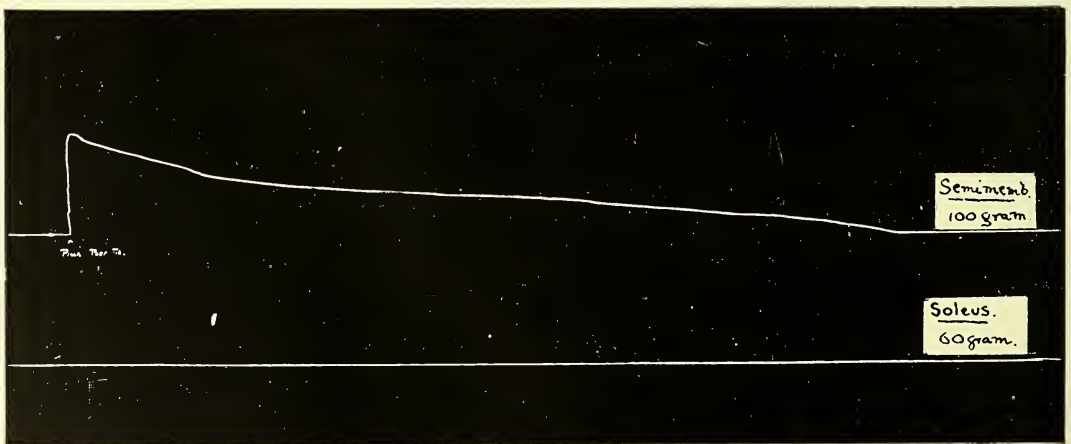


# PLATE III.



Tracing showing the effect of cutting off the blood supply from the red and pale muscles. Rabbit.  
 x—moment of occluding the inferior vena and aorta, 3-30 p.m.  
 3-52 p.m.—pale muscle fails to record.

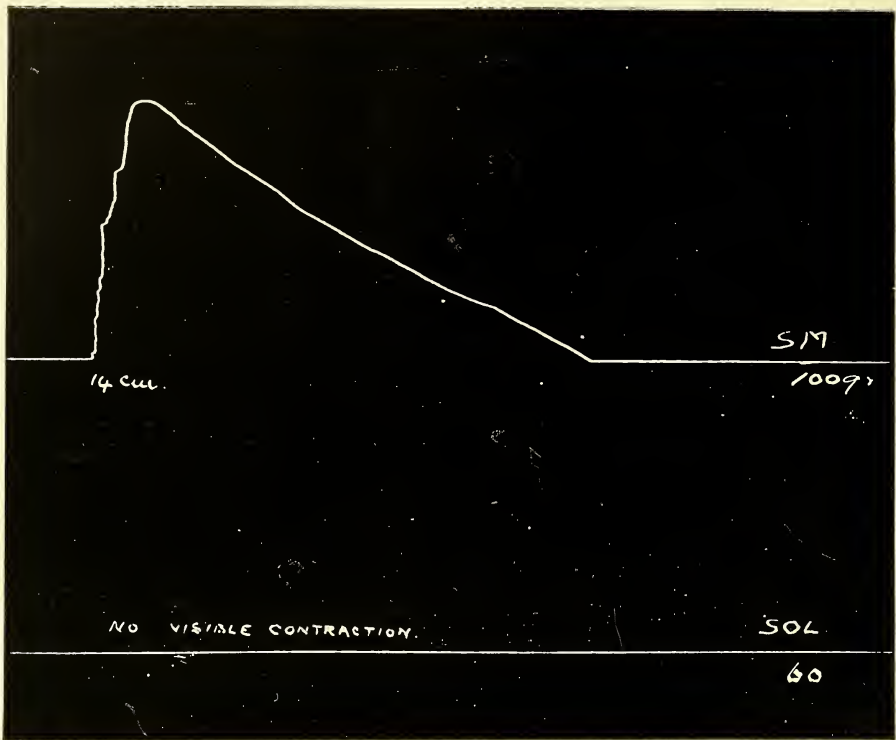
# PLATE IV.



Effect of pinching posterior tibial nerve at the ankle of Rabbit with dissecting forceps. Good reflex contraction from semi-membranosus. No record from the soleus.

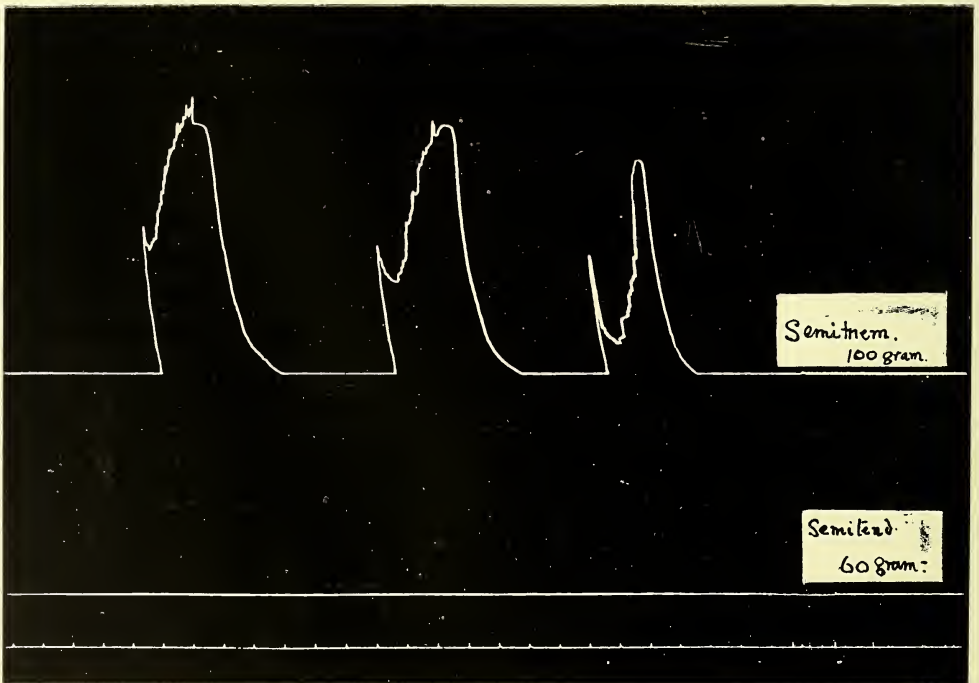


# PLATE V.



Stimulation of posterior tibial nerve of Rabbit by Faradic current. Semi-membranosus gave good response. Soleus quite unaffected.

# PLATE VI.



Stimulation of posterior tibial nerve of Rabbit by Faradic current. Semi-membranosus gave good response. Semi-tendinosus gave absolutely negative result.



EXPERIMENT 5. June 4th. Rabbit, small buck. Prepared as before. Muscles and nerve on right side exposed.

Plate IV.—Tracing shows effect produced by severely pinching the right post. tibial at the ankle with a pair of dissecting forceps. The semi-membranosus gave a good reply, somewhat prolonged. The soleus did not react in the faintest, no movement whatever being observed in the muscle.

The contraction in the semi-membranosus lasted about 50 seconds.

Plate V.—Tracing shows non-reaction of soleus to electrical stimulation of right post. tibial, Faradaic current. No reflex reply from soleus on stimulation of 16 cm. or 14 cm. Faradisation with one cell.

Plate VI.—The semitendinosus was then rapidly exposed and attached to the soleus lever. Post. tibial, right side, was Faradised with secondary coil at 13 cm. Semi-membranosus giving vigorous reply, semi-tendinosus absolutely quiescent. Faradisation of right post. tibial with secondary coil at 10 cm. also failed to elicit a contraction from semi-tendinosus or soleus.

The semi-tendinosus was next isolated entirely, only being attached to the rabbit by the nerve and held up by forceps at its proximal end, so that the faintest change in the muscle could be detected. No stimulus applied to the post. tibial could, however, elicit a response from the semi-tendinosus.

Both the semi-tendinosus and soleus, at the conclusion of the above experiment, contracted vigorously on being directly stimulated by weak Faradisation, or on stimulation of the nerves supplying them.

EXPERIMENT 6. MAY 11th. Buck rabbit. Cord divided, chloroform. Both post. tibials exposed at ankles. Semi-membranosus and semi-tendinosus only partially exposed, so as to interfere as little as possible with the actual blood supply of the muscles. Stimulus of 11 cm. Faradisation, 1 cell. Right post. tibial stimulated, giving marked reflex contraction of semi-membranosus. No sign of contraction in semi-tendinosus. Muscles being bathed as usual in warm saline.

4-26 p.m.—Ten minims 1 per cent. solution strychnia acetate injected hypodermically.

4-30 p.m.—Right post. tibial stimulated, 11 cm. Semi-membranosus went into prolonged tetanus. No sign of contraction in the semi-tendinosus. Rabbit now began to struggle on the stage and then became somewhat quieter.

4-35 p.m.—Right post. tibial again stimulated by Faradisation, 11 cm. General convulsions and death being the result. The semi-membranosus going into tetanic contraction. Semi-tendinosus gave nothing more than some quivers, but no contracting, hardening, or thickening.

*P.M.*—The nerve supply to it was found quite intact, the muscle contracting to stimulation of the sciatic.

EXPERIMENT 7. MAY 11th. Animal prepared as in last experiment. Battery 1 dry cell, induction coil at 10 cm. Faradisation. Previous to this one, Daniel's cell has been used.

3-30 p.m.—Right post. tibial stimulated. Good contraction in semi-membranosus. No contraction in semi-tendinosus.

3-33 p.m.— $2\frac{1}{2}$  min 1 per cent. solution strychnia acetate.

3-38 p.m.—Right post. tibial stimulated. Much more marked reflex in semi-membranosus. No contraction in semi-tendinosus.

3-40 p.m.— $2\frac{1}{2}$  min. 1 per cent. solution strychnia acetate.

3-44 p.m.—Right post. tibial stimulated. Tetanic reflex spasm in semi-membranosus. No contraction in semi-tendinosus.

3-45 p.m.—Death in convulsions, during which the semi-tendinosus was noticed to be contracted. After death the pale semi-membranosus refused to give a reflex contraction even to stimulation Faradic, with secondary coil at 3 cm. It contracted well, however, to direct stimulation of muscle by Faradic current of much less strength.

EXPERIMENT 8. MAY 16th. Rabbit prepared as before, except that the semi-membranosus of the right side was cut entirely away, so that it interfered in no way with the semi-tendinosus, which was well exposed; its under surface left in contact with the adductor magnus, so that the nervous and blood supply were in no way tampered with.

2-30 p.m.—Stimulus to right post. tibial, 10 cm., Faradisation, followed by stimulus of 8 cm. Faradisation. No contraction in semi-tendinosus.

- 2-34 p.m.—2·5 min. 1 per cent. solution strychnia acetate, hypodermically.
- 2-38 p.m.—Stimulus to right post. tibial, 10 cm. Faradic, 8 cm. Far. No contraction in semi-tendinosus.
- 2-45 p.m.—Stimulus to right post. tibial of 10 cm. Faradisation This produced general contraction of all the pale muscles of the thigh, which continued, the semi-tendinosus at first not contracting; in a few seconds, however, the semi-tendinosus also joined in the general contraction. The lever attached to the semi-tendinosus had been raised by the general contraction of the thigh muscles, and still more raised by the contraction of the red muscles. In a few seconds the muscles became quiescent, this being followed by clonic convulsions which soon subsided, leaving the rabbit breathing slowly, pupil reflex present.
- 2-50 p.m.—Stimulus of 10 cm. to right post. tibial produces a small contraction in the semi-tendinosus, 15 min. after strychnine injection.
- 2-52 p.m.—Another similar result obtained.
- 2-53 p.m.—Rabbit died. After death no reflex contraction could be obtained from the semi tendinosus.

EXPERIMENT 9. MAY 18th. Cord divided, chloroform. Rabbit prepared as before. Semi-membranosus and semi-tendinosus exposed. Trachea opened and tube inserted. Stimulation of 10 cm. Faradisation to the right post. tibial. This evoked a well marked contraction in semi-membranosus, none in semi-tendinosus. Pleurae on both sides were then punctured and air blown in. Animal became completely asphixiated in 60 secs. During the convulsive stage no perceptible increase of excitability was noticed in the semi-membranosus, and no contraction in the semi-tendinosus on stimulating the right post. tibial.

Artificial respiration restored the animal, and some time after it was again asphixiated, with the same negative effect on the reflex excitability of the red muscle.

The artificial respiration was continued. The semi-membranosus was next completely removed, and the semi-tendinosus more freely exposed.

- 4-42 p.m.—1 min. 1 per cent. solution strychnia acetate, hypodermically.
- 4-47 to 4-52 p.m.—10 cm. Faradisation to right post. tibial. No change in semi-tendinosus.
- 4-58 p.m.—1 min. 1 per cent. solution strychnia acetate hypodermically.

5-0 p.m.—Same stimulation. No change.

5-5 p.m.—Same stimulation. No change in red muscle; increased excitability in the pale muscles.

5-16 p.m.—1 min. 1 per cent. solution.

5-20 p.m. Same stimulation. Still more marked excitability in pale muscles of thigh.

5-30 p.m.—Same stimulation. Excitability of the pale muscles in thigh was very marked, but there was absolutely no response from the semi-tendinosus.

The secondary coil was then placed at 7 cm., and with this stimulus, a suspicious flicker was noticed, very short in duration, and only observed at the moment of contact of electrodes with the right post tibial.

The semi-tendinosus was then entirely freed, the nerve supply being left intact, and the muscle held up, when, on several occasions, the muscle was noticed to give a little flickering reply to the stimulation of 7 cm. It was in no sense, however, a typical contraction of a red muscle.

EXPERIMENT 10. MAY 23rd. Strong buck. Cord divided, under chloroform. Soleus and semi-membranosus exposed. These muscles were then stimulated by continuous current, descending, produced by a battery of ten dry cells in series. The rabbit being subsequently used to test reflex excitability. The semi-tendinosus was also exposed.

6-5 p.m.—1½ min. 1 per cent. solution strychnine acetate.

6-10 p.m.—12 cm. Reflex excitability of the pale muscles of thigh was much increased, the whole thigh going into tonic contraction. No movement in semi-tendinosus.

6-15 p.m.—Same stimulus, gave very much same result. The soleus was noticed to be giving typical red contractions on stimulation of the post tibial either by Faradisation or by mechanical stimulation—pinching.

6-16 p.m.—1 min. 1 per cent. solution strychnine acetate.

6-23 p.m. Short convulsions of the rabbit. The semi-tendinosus, which is now entirely freed with the exception of its nerve, not contracting, except in two spontaneous, very marked, tonic convulsions, the blood becoming intensely venous in character.



6-45 p.m.— $2\frac{1}{2}$  min. 1 per cent. solution.

6-50 p.m.—Condition the same.

6-54 p.m.—5 min. 1 per cent solution.

6-57 p.m.—Soleus giving good reflex contractions. Semi-tendinosus giving no reflex contractions. Semi-membranosus replying well.

7-3 p.m.—Animal generally convulsed.

7-4 p.m. - Death in one long convulsion, after which no reflex contraction to be obtained from any of the muscles, though they reply to direct stimulation.

EXPERIMENT 11. MAY 25th. Cord divided, chloroform. Soleus and semi-membranosus exposed, also right post. tibial. The minimum stimulus to produce a reflex contraction in the pale muscle was that produced by the secondary coil at 15 cm. Faradisation of the post tibial was followed by faint flicker in semi-membranosus. No reflex contraction in soleus. With secondary coil at 12 cm., there was a sharp contraction in the semi-membranosus, and a slow, feeble contraction in soleus after several seconds stimulation of post. tibial. Secondary coil at 10 cm. gave marked contraction in semi-membranosus, and a slow, typical contraction in soleus. The descending, continuous current was then passed through the two muscles, using at different times 4, 6, or 8 dry cells in series. This was continued for one and a half hours, the muscles being carefully bathed in warm, normal saline all the time.

It was now found that with 15 cm. there was a distinct flickering in the semi-membranosus, but with 12 cm. stimulus there was a marked reply from the semi-membranosus, also the soleus gave a good contraction, more marked than before the passage of the constant current.

With the secondary coil at 10 cm., there was a rapid, strong contraction in the semi-membranosus and a good reflex in the soleus.

It was observed that two or three reflex replies closely following each other inhibited the reflex in the pale muscle, but did not appear to affect the red soleus.

The semi-tendinosus was next exposed, but it refused as usual to give any reflex reply.

The constant current, descending, was applied for 15 minutes with no alteration of the reflex excitability.

EXPERIMENT 12. MAY 27th. Strong Angora buck. Cord divided under chloroform. Semi-membranosus and soleus exposed, and also right post. tibial. Immediately after exposure, a very strong reflex contraction was obtained from the



semi-membranosus by pinching the post. tibial of same side with forceps. The soleus gave no reply.

The secondary coil was then placed at 25 cm. and post. tibial stimulated. The pale gave a reflex contraction, soleus nil. With coil at 20 cm., pale gave marked reflex contraction, soleus nil. With coil at 19 cm., there was a flicker noticed in the soleus.

The Voltaic current was then applied for forty minutes, a various number of cells being used, up to ten in number, after which the non-polarisable electrodes were removed, and Faradisation was employed. With the coil at 18 cm., the soleus gave a distinct contraction, but none with the coil at 20 cm.

No stimulus, mechanical or electrical, would elicit a reflex contraction from the semi-tendinosus.

## APPENDIX (B.)

SHOWING RESULT OF EXPERIMENTS ON REFLEX EXCITABILITY.

Experi- ment.	Stimulus	Condition of Rabbit.	RESULT.		
			RED.		PALE.
			S.T.	SOL.	S.M.
1	Faradisation	Normal	.	—	+
		Strychnine	.	—	+
2	Faradisation	Normal, right	.	—	+
		Normal, left	—	—	+
3	Faradisation	Normal	—	.	+
	Mechanical	Normal	—	.	+
4	Mechanical	Normal	—	—	+
5	Mechanical	Normal	.	—	+
	Faradisation	Normal	—	—	+
6	Faradisation	Strychnine	—	.	+
7	Faradisation	Strychnine	—	.	+
8	Faradisation	Strychnine	+ ?	.	+
9	Faradisation	Strychnine	—	.	+
		Asphixia	—	.	+
10	Faradisation	Continuous Current	—	+	+
		Strychnine	—	+	+
		Mechanical	—	+	+
11	Faradisation	Normal	—	+	+
		Continuous Current	—	+	+
12	Mechanical	Normal		—	+
	Faradisation	Normal	—	+	+
		Continuous Current	—	+	+

S.T. = Semi-tendinosus. SOL. = Soleus. S.M. = Semi-membranosus. — = No contraction.

+ = Reflex contraction. . = No observation,



### Histological Comparison of Nerve Supply to Red and Pale Muscle.

In investigating the nerve supply of these muscles, the points enquired into have been :

1. Relation of the number of nerve fibres to the bulk of muscle in red and pale muscles respectively.
2. Comparing the size of the nerve fibres in each case.
3. Comparing the number and size of afferent fibres in the nerves to these muscles.

The average weights of the semi-membranosus taken from three rabbits was 7·1 grammes, and the average weight of the soleus from the same rabbits was 1·28 grammes, that is the ratio of the red to the pale was 1 to 5·6.

The total number of nerve fibres to these same muscles, was counted, the total being 787 fibres to the soleus and 4187 to the semi-membranosus or as 1 fibre to the soleus to 5·3 fibres to the semi-membranosus.

There is not therefore any marked dissimilarity in the number of nerves to each muscle. If anything the soleus is the better supplied.

The actual numbers were as follows :

	<i>semi-membranosus.</i>		<i>soleus.</i>	
A.	9·8 grammes	1134 fibres	1·6 grammes	276 fibres
B.	6·1       ,,	1134   ,,	1·3       ,,	249   ,,
C.	5·5       ,,	1919   ,,	·94       ,,	262   ,,

The nerves to other solei were counted but the weights of the muscles were unfortunately not preserved. The numbers being 246, 249, 266, 341 and 295, the average when one includes the three above being 273.

Also in the case of the semi-membranosus 2132, 1060, 1143, 784, with the three above gives an average of 1329. These two averages give a ratio of 1 to 4·86. This ratio corresponds fairly closely with the weight ratio of the red and pale muscles. Still if anything the red is the better supplied.

A more interesting point is perhaps the actual size of the fibres supplying the two forms of muscle.





# APPENDIX (C).

		CLASSIFICATION OF FIBRES BY DIAMETER.										
		* Total	18 $\mu$ 17.5 $\mu$	16.5 $\mu$ 16.25 $\mu$	15 $\mu$ 14.5 $\mu$	13.75 $\mu$ 13.5 $\mu$	12.5 $\mu$ 12 $\mu$	11.25 $\mu$ 11 $\mu$	10.25 $\mu$ 10 $\mu$	9 $\mu$ 8.75 $\mu$	7.5 $\mu$	
A.	Soleus ...	246										Smaller than 10 $\mu$ not counted.
	S.M. ...	2132	29	47	1	123	8	73	12	41		" " 8.75 $\mu$ " "
Feb. 3rd. A.	Soleus ...	249										Smaller than 10 $\mu$ not counted.
	S.M. ...	784	3	16	65	75	106	55	11	36		" " 8.75 $\mu$ " "
Feb. 3rd. B.	Soleus ...	266										Smaller than 8.75 $\mu$ not counted.
	S.M. ...	060	1	4	40	97	2	79	6	14	60	" " 7.5 $\mu$ " "
March 5th/30th.	Left Soleus	295										Smaller than 8.75 $\mu$ not counted.
	Left S.M.	1143	5	16	3	6	24	23	47	24		" " " "
March 5th/30th.	Afferent fibres only.											Smaller than 10 $\mu$ not counted.
	Right Soleus ...	121	1	2	1	6	22	13	10			" " " "
Feb. 7th.	Right S.M.	596			41	46	91	28	24			
	Soleus ...	341										
Feb. 1th.	Soleus ...	249										
	S.M. ...	1134										
Feb. 11th.	Soleus ...	276										
	S.M. ...	1134										
Feb. 22nd.	Soleus ...	262										
	S.M. ...	1919										

\* The number expresses the total number of nerve fibres entering the muscle; this number was in each case determined, and the fibres classified by measurement of their diameters.



It was obvious on looking down the microscope even without the aid of a micrometer eyepiece that the cross-section of the fibres to the red soleus was smaller than that of those to the pale semi-membranosus.

The photographs VII and VIII are from cross-sections of the nerves to the pale and red muscles respectively. VII shows the size of the fibres to the semi-membranosus; VIII the smaller size of those to the soleus.

A certain number of the nerves have been measured, and one finds that in the nerves to the soleus one rarely finds any fibres larger than  $13.5\mu$  in some nerves the largest are  $12\mu$ , whilst in the nerves to the semi-membranosus fibres of  $17.5\mu$  or  $18\mu$  are occasionally met with, fibres of  $16\mu$  or  $16.5\mu$  are quite common and fibres of  $15\mu$  very numerous.

In the nerves to four semi-membranosi, which totalled 5299 fibres 2249 fibres or practically one half of the total were either  $10\mu$  or over.

In the nerves to five solei, which totalled 1397 fibres, only 190 fibres, or about one-seventh were  $10\mu$  or over.

Thus one must admit that even after making allowance for possible shrinkage in the smaller nerves, there is a very definite and marked difference in the calibre of the nerve fibres to the two forms of muscle.

Whether this difference will account for the sudden failure of the red muscle to contract to indirect stimulation is hard to say, but one should bear it in mind as a possible cause.

Appended is table showing the result of the nerve counts. App. (C).

Having found that bulk for bulk the red and pale muscles had practically an equal number of nerve fibres in their nerve supply, and that there were definite differences in the size of these fibres it seemed an interesting point to compare the sensory supply to the red and pale muscles.

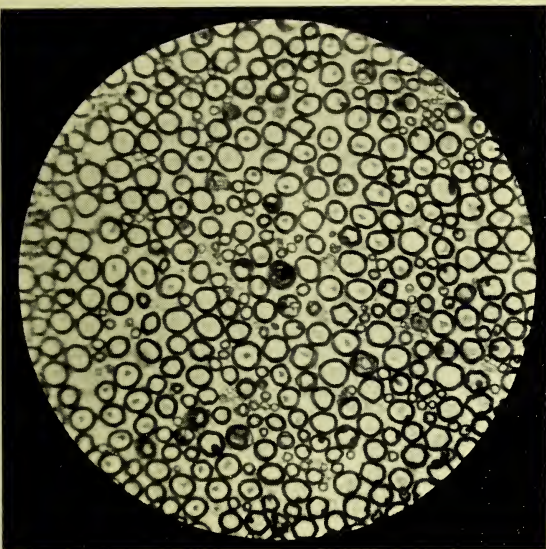
The sensory supply to muscles comprises nerves which end in four forms of end organs. Muscle spindles, Golgi organs, Pacini organs and modified Pacini organs.

Sherrington pointed out that the nerves from these end organs composed one half to one quarter of all the nerve fibres to the limb muscles of the monkey and cat, their size varying between  $18\mu$  and  $2\mu$ .



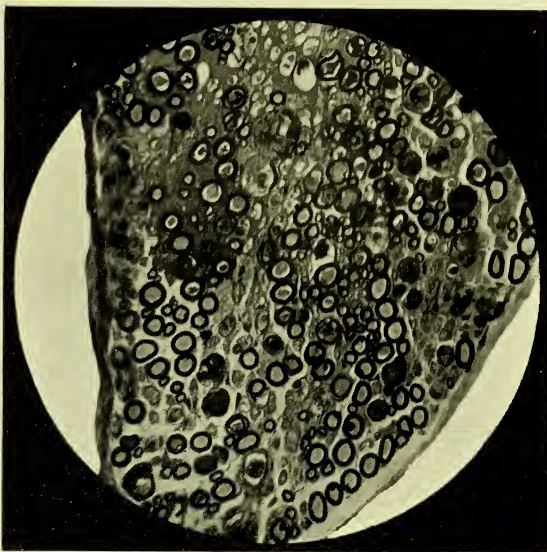


PLATE VII.



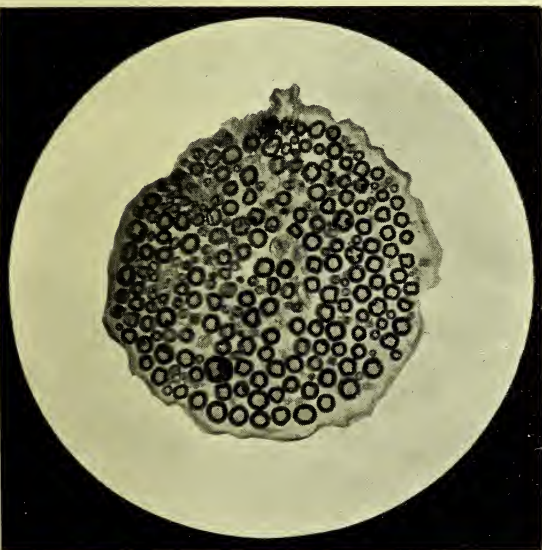
Transverse section of nerve to pale semi-membranosus.  
Rabbit. Osmic acid preparation.  
(Reproduced from untouched microphotograph negative).

PLATE IX.



Transverse section of nerve to the pale semi-membranosus  
after destruction of all efferent fibres. Rabbit.  
Osmic acid preparation. (Reproduction as before).

PLATE VIII.



Transverse section of nerve to the red soleus. Rabbit.  
Osmic acid preparation. VII and VIII the same  
magnification. (Reproduction as before).

PLATE X.



Transverse section of nerve to the red soleus of Rabbit after  
destruction of all efferent fibres. Osmic acid preparation.  
IX and X same magnification. (Reproduction as before).





I decided therefore to destroy the efferent fibres and compare the afferent supply to the red and pale muscles of the rabbit.

Owing to the close attachment of the posterior root ganglia to the dura mater it was impossible to cut through the roots without at the same time damaging the ganglia, therefore I divided the roots intradurally. The 7th, 8th, and 9th posterior thoracic roots were found experimentally to be those supplying the soleus, semi-tendinosus and semi-membranosus, and an attempt was made to divide these roots on the right side in seven rabbits.

Three rabbits died within forty-eight hours from shock. Four lived, nine, twelve, twenty-three and twenty-five days respectively.

These four before being killed were anæsthetized, and their cords divided in the lower thoracic region, the muscles and nerves exposed, and stimuli applied to the sciatic nerve, and also to the nerves as they entered the muscles in case some of the efferent fibres remained, their existence being demonstrated by a slight twitch of the muscle fibre.

To make certain that no efferent fibres had escaped destruction the root ganglia from 6th, 7th, 8th, 9th roots were fixed in osmic acid and cut.

In only one rabbit was the result finally successful, namely, the one in which the rabbit was permitted to live twenty-five days after the operation.

The nerves to the soleus and semi-membranosus in this rabbit were fixed in osmic acid  $\frac{1}{2}$  per cent. and transverse sections cut (*vide* IX—X.).

On counting the number of afferent fibres to the right soleus there were found to be 121 as compared with 295 fibres in the normal nerve to the left soleus.

Supposing that the composition of the nerves to the right and left solei are numerically somewhat similar, then 174 efferent fibres had been destroyed in the nerve to the right soleus. Less than half therefore of the fibres to the red muscle (soleus) were afferent.

The number of fibres to the right semi-membranosus was 596 as compared with 1143 to the left semi-membranosus making a probable 547 efferent fibres.

More than half therefore of the fibres to the pale muscle (semi-membranosus) were afferent.

The number of fibres of  $10\mu$  and over in the nerve to the right soleus was 42, in the nerve to the right semi-membranosus it was found to be 209—practically the old ratio of 1 to 5. This ratio also holds if one considers the whole afferent supply 121 to 596 being 1 to 5.

The conclusion therefore is that the sensory supply to these muscles is practically according to the bulk of the muscle.

Sherrington states that the larger afferent fibres  $7\mu$  to  $18\mu$  are muscle spindle fibres—granting this, then the conclusion is that the spindles also are equally distributed to these muscles, for as we have seen above the large fibres are in the ratio of 1 to 5, that is the number varies as the bulk of muscle substance.

Transverse sections of a considerable number of muscle spindles were examined. No differences could be detected however between the spindles in the red muscles and the pale muscles. Some of the muscles were also prepared according to Sihlers directions and the spindles isolated.

The results so far as the spindles were concerned were not satisfactory the deeply stained nucleated capsule interfering with the definition of the nerve endings in the spindles.

The motor end plates were excellently shown by this method and there was no apparent difference between those of the pale muscle and those of the red.

### Summary of Conclusions.

1. The difference in character and duration of the contraction of the two forms of muscle (red and pale) is due to some essential difference in muscle substance.
2. The red muscles are much better able to resist the cutting off of their blood supply than the pale.
3. The red muscles examined possessed a very low excitability to reflex stimulation, the pale a very high excitability.
4. Bulk for bulk the muscles (red and pale) are supplied with approximately an equal number of nerve fibres.
5. The nerves to the pale muscles are composed of larger fibres than those to the red.
6. Bulk for bulk the muscles (pale and red) have an equal number of afferent fibres.
7. Bulk for bulk there is probably an equal distribution of muscle spindles.
8. No essential differences were found in the nerve endings or in the muscle spindles to the red and pale muscles.

